The Pedological Role of Fungus-Growing Termites (Termitidae: Macrotermitinae) in Tropical Environments, with Special Reference to Macrotermes muelleri

by

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ABSTRACT

The pedological role of termites, and in particular fungus-growing species (Macrotermitinae), is briefly reviewed. Recent work on *Macrotermes muelleri* in the Mayombe Forest, Congo, is then discussed in detail. *M. muelleri* cuts leaves in the litter into small pieces (confetti) which are transported back to the nest. After a few days storage, they are ingested, passed rapidly through the gut where they are broken up physically but subjected to little chemical action, and then they are deposited as mylospheres on the upper surface of the fungus comb. The exosymbiotic fungus, *Termitomyces*, attacks the plant material, especially the "brown pigments" within the leaves, after which it is re-ingested from the base of the comb and subjected to the combined action of enzymes in the termite gut derived from both the termite itself and from the endosymbiotic microflora. The final feces, deposited on the floor of the termites' constructions, are essentially mineral microaggregates with little organic content.

M. muelleri concentrates certain minerals in the nest and nearby soil, but removes a significant amount of organic matter from the environment.

INTRODUCTION AND OVERVIEW

The role of termites in soils has attracted the attention of zoologists and a few agromists for some time but it was not until the 1970's that it was first addressed from a combined zoological and agricultural view point (Lee & Wood 1971a). This paper briefly reviews the subject and then presents in more detail a summary of recent work on the fungus-growing termite *Macrotermes*

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muelleri (Sjöstedt) (Termitidae: Macrotermitinae).

Significance of termites in the consumption of organic matter

In most African ecosystems, termites consume a major part of vegetative production. In the forest of the Zaire basin, Maldague (1964) estimated that termites consumed 6–7 tons of organic matter/ha/yr, equivalent to 50% of the vegetal matter falling on the soil. Lepage (1974), working in the Sahel savanna of northern Sènègal, estimated that termites, especially *Macrotermes bellicosus* (Smeathman), removed 49% of the vegetal production in depressions but only 5% on sandy slopes. Lee & Wood (1971b) indicated a consumption of 35% for some species in Australia (where Macrotermitinae are absent).

All major recent works on organic matter consumption by termites (Abe 1979, Collins 1979, Gupta *et al*. 1981, Josens 1977, Lee & Butler 1977, Matsumoto 1976, Matsumoto & Abe 1979, Wood & Sands 1978) emphasize the influence of termites on the turnover of organic matter in tropical regions. The rate of organic matter consumption by Macrotermitinae varies between 30 and 140 mg per g of termite per day depending on species.

Influence of Macrotermitinae on soil morphology

All authors agree that the material of large epigeal nests is derived essentially from deep soil horizons (Aloni 1975, Bocquier 1973, Boyer 1956, 1973, 1975, Grassé & Noirot 1957, 1959, Harris 1956, Hesse 1955, Leveque 1975, Pomeroy 1976, Roose 1976, Stoops 1964, 1968). Macrotermitinae with a centralized nest use principally the clay fraction (particle size <2μm) for construction. According to Boyer (1982), Macrotermitinae do not occur when the clay content of the soil falls below 10%. The termites select clay according to its plasticity, and hard materials (sand grains) by their dimensions (Grassé 1986). Comparison of numerous species indicates a wide diversity of building materials (soil, feces, organic debris) but the elementary units of construction are more or less the same: ovoid or cylindrical particles 0.2–2.0mm diameter.

The architecture of termitaria has been the subject of a number of studies but few authors have applied soil micromorphholological techniques to the study of termite constructions (Arshad 1981, Barros Machado 1983, Lee & Wood 1971b, Mermut *et al*. 1984, Sleeman & Brewer 1972, Stoops 1964). Recent work by Eschenbrenner (1986) shows that the geochemical and mineralogical characteristics of the mineral particles used by termites closely resemble those of microaggregates of certain ferralitic soils, leading to the conclusion that this microaggregation could be due to "bioaggregation", mainly by termites.

Stone lines at various depths are common in Africa. Some authors consider that biological activity, particularly of termites, could explain their formation (Bachelier & Laplante 1954, Collinet 1969, Gras 1970, Leveque 1969, Raunet 1979, Riquier 1969, Segalen 1969).

Lee & Wood (1971a) calculated that in Australia, mound erosion can result in the formation of a surface horizon 10cm deep in 250-1250 year's.

The possible termite origin of certain iron pans and crusts has been vigorously discussed (Boyer 1975, Erhart 1951, 1956, Grassé & Noirot 1959, Griffith 1953, Saurin & Roch 1958, Tessier 1959, Yakushev 1968) but the question remains unresolved.

Influence of Macrotermitinae on soil physical characteristics

The large epigeal nests of Macrotermitinae are practically impermeable to water despite heavy erosion pressure on them. Some *Odontotermes* spp. construct soil sheeting on the ground surface, some of which is less permeable than the smooth soil surface (Grassé & Noirot 1959). In contrast, some open nests (e.g. those of certain *Protermes* and *Odontotermes* spp.) favor drainage of water deep into the soil (Watson 1969).

The interior of termitaria are much more humid than the surrounding soil due to passive water movement and to the transport of water by termites (Grassé & Noirot 1958a). Boyer (1975) studied the hydrology of the large mounds of *Macrotermes bellicosus* and especially aspects of the movement of water under the mound. During the dry season, engorged layers evaporate slowly because of the microporosity of the materials. The dissolved elements then precipitate, enriching the nest and the surrounding soil.

In terms of the structural stability of the nest material, there seems to be a clear correlation between the proportion of organic matter and resistance to dispersion (Boyer 1975, Bruneau de Mire 1975).

Leprun & Roy-Noel (1976) suggested an edaphic difference between the nests of 2 species of *Macrotermes*: ferrallitic soils with kaolinite in *M. bellicosus*; ferruginous soils with montmorillonite and attapulgite in *M. subhyalinus* (Rambur).

Influence of Macrotermitinae on soil chemical characteristics

The influence of the Macrotermitinae is essentially due to the chemical enrichment of termitaria and subsequently of the surface horizons following the erosion of the nest. Numerous works deal with the chemical composition of termitaria and surrounding soils (e.g. Arshad 1981, 1982, Collins 1979, 1980, Hesse 1955, Kang 1978, Leprun & Roy-Noel 1977, Leveque 1975, Mielke 1978, Nye 1955, Pomeroy 1976, Singh *et al.* 1982, Watson 1975, 1977, Wielemaker 1984, Wood & Sands, 1978). Chemical enrichment of nests is due to the fine particles brought up by the termites, the diverse materials in the water and the deposition of feces. (The Macrotermitinae do not incorporate their feces in their constructions.) The grinding and breaking up by the workers of more or less modified clay material brought from deep down may also contribute to the liberation of certain elements (e.g. Fe, Al, Ca, P, & Mg). Boyer (1975) reported that *M. bellicosus* and *M. subhyalinus* produce illitic type clay by grinding and breaking up silicates of relatively bound aluminum, such as micas. Pedologists agree that clays and micas used by these large termite builders are modified by their action and by conditions in the nest (Boyer 1982, Leprun & Roy-Noel 1976, 1977, Sys 1957).

The influence of large epigeal nests on the chemical characteristics of soils is more important than that of subterranean nests, which are characterized by a more superficial origin of the nesting materials.

Boyer (1956) found less organic material in the nests of *M. bellicosus* than in the surrounding soil in the Central African Republic. In contrast to soil feeding termites, the organic matter in the nests of Macrotermitinae is largely not of fecal origin but comes from the upper soil horizons.

In Zaire, the soil of the large mounds of *Macrotermes* spp. ha~~ve~~s very fine texture, clearly lower levels of carbon and nitrogen than in the surrounding soils, and little modified C/N ratios (Maldague 1959). The epigeal termitaria exhibit an increased cation fixation capacity (T) related to a much greater clay content, but like the increase in the sum of exchangeable cations (S) which is generally greater than that of the fixation capacity, the S/T ratio~~s~~ is normally found to be much higher than in the soil (Goodland 1965, Lee & Wood 1971b, Stoops 1964, Sys 1957, Thorpe 1967). In large epigeal mounds numerous works record higher levels of total bases, exchangeable bases, and sometimes calcium and soluble salts, derived from the bedrock (Boyer 1956, Becker & Seifert 1962, Stoops 1964, Watson 1970, 1972).

Layers of calcium carbonate nodules have often been found deep in large epigeal termitaria, even in areas of low calcium ferralitic acid soils, but there is no clear explanation of this phenomenon (Boyer 1956, Hesse 1955, Nye 1955, Pendleton 1941, Roonwal 1975, Sys 1957, Watson 1962).

The pH of the mound soil is either little modified or close to neutrality (Boyer 1956, Goodland 1965, Nye 1955, Sys 1957, Watson 1962). The chemical richness of the nests, their generally less acid pH, and their frequent modification with applications of saliva appear to slow down the processes of ferrallitization; the ratio of SiO_2/Al_2O_3 is often much greater in the nests than in the surrounding soil. Free silicon could be transported by water and held in the nest. Humidity in the nest remains high during the dry season due to water transported by workers from more or less permanent water tables (Grassé 1986).

The harshness of the environment is moderated within termitaria. Illites from mica do not kaolinize and montmorillonite sometimes exists in small quantities within the large epigeal nests, its presence not explained by the transporting activities of the termites. Various authors have considered the possible synthesis of montmorillonite within the nest (Fripiat *et al.* 1957). Magnesium could favor synthesis of Montmorillonite and calcium could retard kaolinization. No recent work has taken up this hypothesis. pH is significant in the synthesis of different clay minerals, regulating the speed of dissolution and precipitation of various constituents of phyllite (Boyer 1975, 1982, Lee & Wood 1971a, b, Leprun & Roy-Noel 1976, Sys 1957, Watson 1967).

Macrotermes muelleri

Introduction

Our knowledge is lacking on the role of termites in the process of humification of the organic matter of the hemi-organic horizons. For this reason, a study of the action of termites on the transformation of organic debris in a humid tropical forest (Mayombe Forest, Congo) has been undertaken, comparing several termite species with different feeding regimes (Garnier-Sillam 1987). Only the fungus growing *M. muelleri* is discussed here. The following approaches were taken:

1. Chemical study, coupled with transmission electron microscope (TEM) observations, permitting an understanding of the characteristics of the initial food material and its modification during transit through the gut (bolus of food and feces).

2. Pedological analyses of organo-mineral samples linked to studies of the activity of this species which constructs an extensive network of galleries in the soil, thus permitting a better understanding of the physico-chemical transformations of hemi-organic horizons resulting from the building and feeding behavior of the termites.

M. muelleri is a leaf-cutter found in equatorial African forests. It forages in thousands both at night and during the day in subterranean galleries opening from 3-30m from the nest. Major workers, accompanied by major and minor soldiers, cut up leaves out in the open (generally brown leaves strewn on the soil surface) into "confetti" of 3-4mm diameter which they carry in their mandibles back to the nest via subterranean galleries. The confetti is stored in chambers in the nest. After a few days, the workers eat this stored vegetal matter. It passes relatively quickly through the anterior and middle parts of the digestive tract, arrives in the hind gut where it stays a short time, and finally passes into the rectum and is expelled as a "mylosphere" (Grassé 1978). Mylospheres are completely different from feces. They are deposited on the upper part of the fungus comb.

The fungus combs possess a well defined texture and architecture characteristic of the species. They can usefully serve as specific characters (Grassé & Noirot 1958b). The fungus combs of *M. muelleri* look like flat cakes crossed by vertical holes. White bodies (masses of conidiophore filaments in the form of spheres - Heim 1977) appear in these holes. These are mycotetes (Bugnion 1910) of the basidiomycete fungus, *Termitomyces* (Agaricacea) characteristic of the Macrotermitinae. Several other fungi, particularly *Xylaria* spp., live in the comb but do not proliferate nor produce fruiting bodies or spores unless the environment is modified (for example by experimental removal of the comb from the nest) (Thomas 1987). The older whitish lower surface of the comb is eaten by the workers and hence is not covered by a layer of mycelia. They thus ingest material which has been subject to the prolonged action of *Termitomyces*. Grassé & Noirot (1958b) and Josens (1977) have shown that the comb is in perpetual transformation due to the double action - construction and consumption - of the workers.

Study of metabolism

We have studied successively the leaves, fungus comb comprised of mylospheres, and feces of *M. muelleri* (Garnier-Sillam 1987, Garnier-Sillam *et al*. 1985a, b, 1988a, b).

Leaf Fragments

Leaves are made of cells with cellulose walls (epidermis, parenchyma, vascular bundles) and of lignified tissue (secondary xylem, sclerenchyma) essentially located in the veins. The brown color of the leaves is due to the formation during senescence of intracellular "dark brown products" when vacuolar phenolic compounds come into contact with cytoplasmic proteins. These brown pigments represent about 30% of the dry weight of the leaf and contain 50-60% of the total nitrogen. Lignin represents about 10% and cellulose and hemicelluloses 35-40% (Toutain 1981). The 3 principal organic components (pecto-cellulose walls, lignin thickenings, and brown pigments) are readily identified under the TEM. Numerous free-living bacteria have been observed in the different structures but not 1 mycelial filament nor unicellular yeast-like element has been seen.

Fungus comb

The fungus comb, constructed from mylospheres produced by workers, contains no bacteria or mineral particles. TEM observations of the mylospheres in the comb matrix show that the rapid intestinal transit has broken up the leaf cells.

In the comb, *Termitomyces* perforates the pecto-cellulose leaf cell walls in order to degrade and transform in particular the brown pigments (polyphenol proteins) within the cells. Consequently, the comb has a brown appearance on its upper parts, gradually whitening towards its base.

Feces - organic matter transformation in the intestine

Digestive tracts of 200 workers from all parts of the nest have been studied. No rectal bulb contained mylospheres. Ultrastructural observations indicated 2 types of feces in the minor workers, 1 of high mineral content, the other low. However, those of low mineral content did not correspond to mylospheres with respect to the state of degradation of organic structures and the presence of mineral particles. All major worker feces observed contained many clay particles. This could be related to worker polyethism, though this need experimental confirmation, with major workers only having contact with soil materials (Badertscher *et al.* 1983). In general, biodegradation of the various organic fragments seen in the feces is always very advanced. The cell walls are partially replaced by electron opaque granulo-fibrillic structures. The lignin thickenings show large regions of lysis often with bacteria present. The various brown pigments show clear fragmentation due to the action of exoenzymes. The biodegraded organic matter, generally granular in form, is mixed with the clay particles, forming the matrix. This latter constitutes an important fraction of the feces. Dead mycelial hyphae and numerous bacterial colonies are enclosed in an envelope of clay particles. The connections between the mineral material and the poorly polymerized organic matter are formed exclusively in the digestive tract.

The three way symbiosis, fungus-bacteria-termite

This study shows that the fungus-bacteria-termite symbiosis appears to be established by a process that differs from that described by others. The exosymbiotic fungus, *Termitomyces* , perforates the pecto-cellulose plant cell walls in order to reach the masses of brown leaf pigments. This therefore proves its cellulolytic, pectinolytic, and perhaps its ligninolytic activity. Essentially the fungi's action is to transform profoundly the brown electron opaque substances, leading to their disappearance. Subsequently, the enzymatic arsenal of the digestive tract, derived from both the termite and bacteria, prolongs the action of the fungus so that all the organic components, including lignin, are degraded.

In this way, on leaving the digestive tract, the various organic fractions have been subject to the triple action of fungal, bacterial, and termite enzymes. They are greatly transformed and the organic residues constituting feces, are deposited on the floor of the constructions and on the soil. These are comprised principally of biodegraded granules.

Role of *M. muelleri* in organic matter biodegradation

The metabolism of *M. muelleri* can be summarized as follows:

1. The passage through the gut which leads to the formation

of mylospheres (deposited on the upper surface of the fungus combs) has the effect, visible under the electron microscope, of mechanical micro-division of the organic fragments; chemical action on the superficial leaf cell layers may also occur.

2. The exosymbiont (*Termitomyces*) alters the pecto-cellulose walls and perhaps the lignin thickenings but its action is above all directed to the brown pigments which it degrades and transforms.

3. Ingestion of the lower, paler parts of the fungus comb (leading to feces deposited on the floor of the constructions) has as its consequence: (i) enzymatic decomposition in the intestine by enzymes from both termite and symbiotic microflora, acting on the pectocellulose membranes, the lignin thickenings, the organic polycondensates (polyphenol proteins), the mycelial filaments and certain bacterial cytoplasm; (ii) production of polysaccharides, originating from either enzymatic biodegradation of vegetal matter or products secreted by the bacterial microflora; (iii) chemical synthesis, by polycondensation of aromatic components, in association with various other components (peptides, polysaccharides) which, in contact with the mineral fraction, form an organic material closely bound to mineral.

A chemical study of the organic material, following the method of Bruckert (1979), allows the alkaline soluble humic components to be separated from the nonextractable humified fraction which is designated globally by the term humin. This, followed by an ultrastructural study of the humified fraction, indicates that the organo-mineral connections apparent in *M. muelleri* workers' feces are weak (easily broken under the action of the extraction reagent, sodium pyrophosphate). This suggests that the organic fecal material deposited on the floor of the constructions is easily mineralized (ratio of fulvic to humic acids in the feces is approximately 3.2; Garnier-Sillam 1987).

Influence of *M. muelleri* on global humification processes and the biogeochemical cycles of tropical forest soils

The upper horizons 2m from the nest are comprised of a litter layer (0.5-0.8cm deep) which lies directly on a mineral horizon A which is very slightly humified and no more than 7cm thick. With no transition, horizon B1, of a clay-silt texture and 12-15cm thick, follows horizon A. Some subterranean galleries (1-4cm wide) of *M. muelleri* are present.

In the neighborhood of the nests of this species, the soil is modified to a depth of 80cm or less. A homogeneous distribution of mineral particles is established but one cannot say whether this is due to the activities of the workers of existing colonies or the successive action over time of many colonies in the same place.

The wall of the nest, particularly the internal structure, is composed of a high proportion of fine mineral particles (ca. 42% clay) and has a total iron, aluminum, and exchangeable cation content greater than control horizons of nearby soils. The higher clay proportion in the superficial horizons and in the walls is due to materials brought from deep in the soil by the workers.

The mobilization of the biogeochemical cycles has many origins: (i) as a result of the workers' deep mining the nest is enriched in cations and sesquioxides; (ii) the high humidity of the wall, supposing that transport of bases and mineral elements in solution is favored by the movements of water, is the basis on which the nest rests (through recovery of runoff water and through workers transporting water from the underlying water tables); (iii) by the recovery, in the feces deposited on the floors of all constructions, of an important part of the biological material ingested.

The workers of *M. muelleri* remove a significant amount of organic material. According to the figures given by Josens (1977) and Lepage (1979), one can estimate that in the area studied this species consume 3.5-4.0 tons of leaf material/ha/yr.

CONCLUSION

M. muelleri plays a major role in biogeochemical cycles by augmentation of the total and exchangeable mineral reserves of the surface horizons. The successive and seemingly synergistic degradative action of the enzymes of the exosymbiotic fungus, the termites themselves and the endosymbiotic microorganisms leads to a profound transformation of leaf material. Only a very small quantity of organic matter is finally returned to the ecosystem.

This trophic system has important repercussions on the chemical properties of soils. The horizons around the nest of *M. muelleri* are impoverished of carbon. Leaves are intensively removed from the litter and the return of organic matter to the soil is poor. Furthermore, the organo-mineral microaggregations formed during passage through the gut of *M. muelleri* are not as stable as the microaggregations formed by soil feeders (cf. *Thoracotermes macrothorax* (Sjöstedt) - Garnier-Sillam 1987, Garnier-Sillam *et al*. 1988c) on account of the poorly humified character of the vegetal substrate. The possibilities of chemical connections with the mineral supports are weaker; clay no longer acts as protector of the organic matter which therefore mineralizes readily.

In consequence, a significant quantity of organic material removed from the ecosystem is held for some time in the fungus combs and subsequently metabolized. For a large part, it plays but a minor role in the development of clay-humic complexes. The reduction of organic material in the horizons disturbed by *M. muelleri* can, beyond a certain threshold often attained in tropical forests, have grave consequences for the characteristics of the absorbing complex of the humiferous horizons. It is in this way that the properties of soils influenced by *M. muelleri* are greatly perturbed.

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